From maternal investment to lifetime maternal care

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Chapter 14 From Maternal Investment to Lifetime Maternal Care

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All female mammals provide energetic investment in their offspring in the form of gestation and lactation. Primates stand out among mammals, however, in that the mother-offspring bond rarely ends at weaning. This is a result of their general gregariousness and relatively slow development (chapter 10, this volume). In fact, the potential for prolonged investment in some form exists as long as mother and offspring survive and inhabit the same home range, and especially when they belong to the same social unit. Maternal support may be prolonged throughout the mother's life span and may even be expanded to include grand-offspring (Fairbanks 1988, 2000). Indeed, despite being weaned, juvenile primates, who are still relatively small (initially on average about 30% of maternal weight: Ross 2003), require the "umbrella" care provided by the mother and other members of her social group. Such care is often shared with (half)-siblings of various ages. It provides the offspring not only with antipredator and social protection (thus improving its chances of survival and access to food), but also with numerous opportunities for social learning, and it sometimes includes possibilities to obtain food directly from the mother or other group members. In some species it even includes being carried, and active food sharing by others than the mother. Thus, in addition to the basic direct physical investment shared with all other mammals (e.g., nursing, carrying, thermoregulation), primate mothers also offer their offspring prolonged social care (agonistic and antipredator protection, learning opportunities; see chapter 11, this volume). The long association between mother and offspring, which is even further extended for the philopatric sex, provides great potential for long-term maternal influence on offspring fitness.

Trivers (1972) defined *parental investment* (PI) in terms of the cost to the parent, so that it reflects any parental expenditure of time and energy that reduces the parent's ability to invest in other offspring. The broader term *parental care* includes any parental behavior and expenditure that is likely to increase the offspring's chances of survival and success (Clutton-Brock 1991). Parental care can be depreciable—that is, it contributes exclusively to the offspring concerned because the relevant resource is reduced in availability to others as it is allocated. Examples of this include carrying, food provisioning, and unilateral agonistic support in conflicts. Care can also be nondepreciable—that is, the relevant resource is not reduced in availability when invested, and thus is potentially shareable across multiple offspring at the same time. Examples of this form of care include vigilance and facilitation of opportunities for learning.

In this chapter, I examine variables that affect *maternal investment* and *care* throughout an offspring's life, such as the commencement of reproduction in relation to maternal condition and environmental fluctuations; the interactions between mother and offspring during gestation and lactation; the opportunities for maternal care beyond weaning; care by others; and the possibility of differential investment and care in sons versus daughters. Before examining these issues in detail, however, we must deal with two general issues that characterize all interactions surrounding reproduction. First, reproduction is an arena of evolutionary conflict

that occurs not only between mothers and offspring, but also between the two parents and among offspring (Trivers 1974; Parker et al. 2002). Second, because maternal energy expenditure on behalf of the offspring cannot usually be measured directly in wild primates, we must address the indirect measures that are available to field workers.

Conflicts of Interest

As in other mammals, female primates carry the entire burden of energetic investment in offspring through gestation, and the lion's share during lactation (fig. 14.1). How much energy a mother provides to each offspring is likely to affect her own survival chances, as well as those of her offspring, and therefore her own lifetime reproductive success. Because a younger sibling is at best a full sibling to the current offspring, the latter should prefer more and longer investment directed to itself than to its future sibling. The mother, however, is equally related to all her offspring. Thus, throughout development there is a potential conflict between mother and offspring about how much she invests in them and when she should end this investment (Trivers 1974; Clutton-Brock 1991).

Despite the potential for conflict, mother and offspring obviously share an interest in ensuring that maternal investment not only allows the infant to survive and ultimately reproduce, but also (at least in primates) allows the mother to survive to provide important postweaning care. Such care can hardly be enforced by the offspring, since the mother can refuse to provide it if the attendant costs are too high. Thus, in primates the potential for conflict largely ends with weaning, whereas prolonged care is often expected.

Less visible than the behavioral conflict over the timing of termination of exclusive investment is the physiological tug-of-war between mother and offspring in utero (see below). This chemical interaction affects the fetus's physiological settings, and also turns out to influence its lifelong responses to food availability, social stress, and thus susceptibility to disease. Another major conflict hidden in utero is that between the two parents. Paternal copies of genes may be selected to stimulate the developing fetus to maximize its extraction of resources from the mother, whereas the mother's gene copies are expected to limit investment to a lower level that optimizes the mother's lifetime reproductive success (Moore & Haig 1991).

A group-living primate mother typically combines investment in her youngest offspring with supplemental care for older offspring of various ages, which still live in association with her. During the relatively long postweaning immature phase of primates, there is ample opportunity for competition among siblings of different ages. In such conflicts, primate mothers tend to support the younger, weaker offspring against their own stronger siblings, resulting in the "youngest ascendancy dominance rank acquisition" in matrilineal social groups (Kawai 1965, see also chapter 21, this volume).

Measuring Maternal Investment and Its Impact

It is very difficult to estimate maternal investment directly. One approach to measuring it noninvasively is to record a mother's activity pattern during the various phases of reproduction, and to estimate the cost of provided care in comparison with that of nonmothers (or of the same female in the nonreproductive state). However, under natural conditions many other factors vary over time, and reproduction may be timed to take advantage of this variation. Thus, only a few dedicated studies under natural conditions have used this method of estimating the costs of gestation, milk production, carrying, and so on in primates (e.g., baboons, *Papio* spp., Altmann 1980, Dunbar 1988, Barrett et al. 2006a; spectral tarsiers, *Tarsius tarsier*, Gursky 2002; siamangs, *Symphalangus syndactylus*, Lappan 2009).

It is easier to estimate the cost to the mother in terms of time invested exclusively in a particular offspring or litter by measuring interbirth interval (the intervals between the birth of one infant surviving at least to weaning and the next birth). Within a species, gestation length varies very little (Martin 1990), but the duration of the lactation period varies within and among individuals and populations. Similarly, variation is found in the overlap between lactation and gestation of the next offspring, or even the duration of a distinguishable recovery period for the mother to reach a condition threshold for conceiving again (Bercovitch 1987; Mas-Rivera & Bercovitch 2008). In all scenarios, variation in interbirth intervals provides a reasonable estimate of differences among females (or conditions or populations) to acquire enough energy to raise healthy, surviving offspring (e.g., baboons: Altmann & Alberts 2003, 2005; Garcia et al. 2009; long-tailed macaques, *Macaca fascicularis*: van Noordwijk & van Schaik 1999). Similarly, differences in the cost of raising sons or daughters to weaning age can be estimated through the duration of the subsequent birth intervals (see below). Time will therefore be the currency used here to compare maternal *investment* across conditions and species.

Obviously, time cannot be used to estimate the quality of post-weaning *care*. Maternal care is recognized by its value to the offspring, thus it should improve the survival and reproductive success of the offspring. Since many fac-

Fig. 14.1. In almost all monkeys and apes, infants experience relatively long periods of dependence on caregivers, both for nourishment and for locomotion. With a few notable exceptions, it is mothers that bear the burden of most of these costs, such as this female ursine howler monkey (*Alouatta arctoidea*) in Hato Masaguaral, Venezuela. Photo courtesy of Carolyn M. Crockett.

tors could influence the offspring's success in life, one can isolate the influence of maternal care by a comparison of the survival and success of orphans with that of immatures living in association with their surviving mothers (see below).

Maternal Investment and Maternal Condition

Access to Food

Mothers need to find the balance between reproduction and the growth and maintenance needed for their own survival (age-related investment decisions are discussed in chapter 10, this volume). Studies of food-enhanced primate groups show that females with access to more food (enhanced maternal condition) invest more heavily in reproduction. This is shown by their faster-developing offspring and shorter interbirth intervals (e.g., Japanese macaques, *Macaca fuscata*, Watanabe et al. 1992, Kurita et al. 2008; yellow baboons, *Papio cynocephalus*, Altmann & Alberts 2005). Under natural conditions, a mother's social status mediates access to food for herself and her offspring. Indeed, high-ranking females often have larger and/or faster-growing infants, which are weaned after a shorter lactation period (e.g., baboons, Johnson 2003; Altmann & Alberts 2005; Garcia et al. 2009). This results in a shorter interbirth interval after a surviving offspring (e.g., macaques, Sugiyama & Ohsawa 1982, van Noordwijk & van Schaik 1999; mandrills, *Mandrillus sphinx*, Setchell et al. 2002; chacma baboons, *Papio ursinus*, Cheney et al. 2004, 2006), and faster-maturing daughters (lower age at menarche and first reproduction: vervet monkeys, *Chlorocebus pygerythrus*, Cheney et al. 1988; macaques, Bercovitch & Berard 1993, van Noordwijk & van Schaik 1999; mandrills, Setchell et al. 2002; baboons, Bercovitch & Strum 1993, Johnson 2003, Altmann & Alberts 2005). Thus, variability in interbirth interval, in offspring weight or age at weaning, and in age of sexual maturation indicates differences in the rate of a mother's investment in her offspring, and is closely linked to access to food (see also chapter 15, this volume).

Timing of Reproductive Events

Few if any mammals experience a continuous food supply. Fluctuations in food availability and quality often come in rather predictable yearly cycles, but they can also be less predictable, with pronounced interannual variation (van Schaik et al. 1993; chapter 7, this volume). Since female reproduction is largely dependent on access to sufficient food, it is important to understand how females time their reproduction relative to periods of food abundance and (unpredictable) shortage. Primates tend to have a long reproductive cycle, with an especially long lactation period in comparison to other mammals of similar size (chapter 10, this volume). Thus, mothers need to schedule conception so that peak needs (during lactation) will coincide either with a future peak in food availability or with built-up internal (fat) reserves that buffer for low food supply. Either way, limiting the onset of reproduction to a particular season is potentially costly to females, since a reproductive failure would necessarily delay subsequent breeding. Thus, seasonal reproduction must have compensatory benefits in order to be favored by selection, although those benefits do not necessarily reflect the same reproductive strategy in all seasonally breeding primates.

Seasonal breeding is common in most taxonomic groups, but it follows different scenarios in different species. Drent and Daan (1980) identified two distinct reproductive strategies in birds that breed at high latitudes. In some species, the females store fat before the onset of reproduction and adjust the number of eggs they lay to these reserves. Conversely, the females of other species do not store fat in advance, but instead dynamically adjust their clutch size to their food intake rate. A similar distinction in reproductive scenarios was independently proposed for tropical primates, inspired by the high interannual variance in fruit abundance in Southeast Asia as compared to more predictable seasonal variation in food availability in other regions (van Schaik & van Noordwijk 1985). Stearns (1992) incorporated these different investment scenarios into general life-history models to explain variation in the number of offspring produced, the timing of the reproductive cycle, and two extreme maternal strategies of energy acquisition

to support reproduction. Mothers following the *income breeding* scenario completely support their reproduction through daily foraging, whereas those following the *capital breeding* scenario store reserves whenever possible, mostly before and during gestation, to support lactation even when conditions are suboptimal.

With few exceptions (e.g., hooded seals, *Cystophora cristata*, which have an extremely short lactation period: Iverson et al. 1995), mammals cannot sustain lactation on built-up fat reserves alone. Therefore, instead of defining a strict dichotomy in breeding scenarios, the labels *income* breeding and *capital* breeding mark the endpoints of a continuum that ranges from species that use only an external trigger for the onset of (seasonal) reproduction irrespective of physical condition to species that require a minimum maternal condition before conception (and additional fat storage whenever possible). This continuum has been helpful in explaining the variation in temporal patterns of maternal investment in many mammals (e.g., Festa-Bianchet et al. 1998; Boyd 2000; Broussard et al. 2005; Wheatley et al. 2008), including primates (e.g., Richard et al. 2002; Brockman & van Schaik 2005; Janson & Verdolin 2005; Lewis & Kappeler 2005). There is little evidence that maternal condition affects litter size in primates since most species give birth to single offspring. However, for species in which twins and triplets are common, females in better condition are more likely to produce triplets, at least in captivity (common marmosets, *Callithrix jacchus*, Tardif & Jaquish 1997, Nievergelt & Martin 1999; ring-tailed lemurs, *Lemur catta*, Pereira et al. 1993, Nunn & Pereira 2000).

Even though detailed data on female fat storage are lacking for most primate species, the available empirical evidence is consistent with the income-capital continuum perspective (table 14.1; see also evidence presented in Brockmann & van Schaik 2005). First, income breeders undergo a very small number of ovarian cycles before conception, whereas that number is variable in capital breeders, which have a high maternal condition threshold.

Second, income breeders tend to have lower frequency of failed pregnancies (abortions), and are instead more vulnerable to high rates of infant mortality (e.g., ring-tailed lemurs, Gould et al. 2003; Japanese macaques, Kurita et al. 2008) or increased rates of infant rejection and abandonment by mothers in poor condition (e.g., vervet monkeys, Fairbanks & McGuire 1995).

Third, income breeders tend to wean infants at a particular absolute age and relative to a temporary food peak, which allows the mother to align her next conception to the following year's food cycle. Thus, we expect to find a less variable interbirth interval or a bimodal distribution. At the capital-breeding end of the continuum, infants are weaned once they have reached a certain condition. Here, length of lactation (age at weaning) and thus interbirth intervals tend to be more variable among females, whereas weight of the weanling is less variable (e.g., baboons, Lycett et al. 1998, Johnson 2003, Altmann & Alberts 2005, Barrett et al. 2006b, Cheney et al. 2006, Garcia et al. 2009; Phayre's leaf monkey, *Trachypithecus obscurus phayrei*, Borries et al. 2008; white-faced capuchins, *Cebus capucinus*, Fedigan et al. 2008; siamangs, Lappan 2008).

Fourth, income breeders using an external trigger continue to reproduce seasonally when translocated or provisioned with a constant diet (e.g., common squirrel monkeys, *Saimiri sciureus*, Schiml et al. 1999; lemurs, Rasmussen 1985). Capital breeders show more variation in seasonality between populations and become less seasonal in their

Table 14.1. Maternal parameters expected under the extreme scenarios of the income-capital continuum (cf. Brockman & van Schaik 2005)

	Income scenario	Capital scenario
Maternal physiology	Little fat storage	Fat storage whenever possible, especially during gestation
Ovarian cycles to conception	Few	Variable
Ovarian activity: Conception	Triggered by exogenous factor (e.g., photoperiod)	Triggered by endogenous factor (physiological condition)
Maternal recuperation period	None	Variable after raising of offspring to weaning
Mating/birth seasonality	Pronounced seasonality	No strict seasonality
Effect of translocation or provisioning on reproduction	Same external trigger, same seasonality	Less seasonality
Timing of gestation	Preceding predictable high food availability	During high food availability
Timing of lactation	Before and during high food availability	During and after high food availability
Timing of weaning	During high food availability	Delayed if food availability insufficient
Birth rate	Annually or semiannually; low interannual variation	High interannual variation depending on food/body condition
Abortion rate	Low	Higher, affected by food acquisition
Infant mortality	Food-dependent	Relatively low
Effect of maternal dominance rank	Little effect on birth rate, some effect on infant survival	Variable effect on birth rate and age of weaning through maternal condition; also possible effect on infant growth rate

reproduction under provisioning or after translocation to a less seasonal environment (e.g., baboons, Barrett et al. 2006; long-tailed macaques, Kavanagh & Laursen 1984).

Finally, the income-capital continuum also helps us to understand differences between populations in the changes that take place in maternal activity budget during pregnancy and lactation. More seasonal and income breeders have to increase their intake (or decrease their expenditure) during lactation, whereas at the capital breeding side of the spectrum, fluctuations in activity budget will be less pronounced (cf. Altmann 1980 vs. Barrett et al. 2006a).

On average, female reproductive physiology is expected to take advantage of predictable changes in food availability. With lengthening of the reproductive cycle and decreasing predictability of the environment, however, a mother needs to provide a buffer to ensure a regular flow of nutrients to her developing offspring. This constraint has led to variation among primates in the timing of reproduction relative to changes in the environment, as well as variation in patterns of maternal physiology and reproductive failure.

Prenatal Investment: Gestation

Mother-Fetus Interaction

During gestation, a mother hosts her offspring inside her own body and allows it to grow by taking nutrients from her. The exchange of nutrients and waste products between mother and offspring takes place through the placenta, an organ formed by the fetus. The anatomical details of the placenta's connection with the uterus vary among mammalian taxa, with three distinct types of fetal invasion of maternal tissue. The least invasive type, epitheliochorial placentation, is found in the strepsirrhines. Through special glands in the uterine wall, the mother releases nutrients for diffuse exchange over a large area of contact between maternal and fetal tissue. All other primates have haemochorial placentation, characterized by fetal tissue entering the uterine wall and connecting directly to maternal blood vessels. The degree of invasiveness varies, however, and it appears to be lowest in the platyrrhines (Carter 2007). Martin (2008) concluded that both these forms of placentation are derived from the intermediate ancestral endotheliochorial form, but that there is no evidence for a difference in efficiency (as estimated by fetal growth rate), and that precocial and large-brained offspring can be produced irrespective of placental anatomy. Thus, the demand of a higher fetal brain growth rate seems not to have been the selective force that resulted in the two extreme forms of placental organization of the two major primate lineages. However, some differences in vulnerability to pregnancy complications may be related to these anatomical differences.

A mother's offspring is related to her by only 50%, so her body needs to suppress a strong immunological response to reject the implantation of such a foreign body inside her uterus. It is possible that this suppression needs to be even stronger in species with closer contact between maternal and embryonic/fetal tissues (especially in species with invasive haemochorial placentation, such as the Cercopithecoidea and Homoinoidea). However, variation in such a maternal immunological response is still poorly documented (Martin 2008).

After implantation, the intimate mother-fetus relationship may be shaped partly by an evolutionary conflict between the maternal and fetal cells over the quantity and rate of maternal nutrients taken by the fetus (Haig 1993). The fetus is expected to prefer greater access to maternal resources than the mother is willing to allow. Within the fetus, paternally "imprinted" genes are expected to counteract maternal mechanisms that limit investment in the fetus, which ultimately reflects sexual conflict. The interaction between opposing chemical signals from mother and fetus also serves as information exchange, indicating the competence of the fetus and the limits of maternal abilities to provide nutrients (Haig 1993), either from reserves or ongoing food acquisition.

The intimate and prolonged contact between cells with different genetic backgrounds also requires a carefully balanced interaction between the fetal and maternal expression of (species-specific) major histocompatibility complex (MHC) genes in order to avoid severe harm to mother or offspring from a suboptimal exchange of nutrients and information, or even from premature expulsion of the fetus itself (Bainbridge 2000). The haemochorial placenta releases an array of chemical stimuli directly into the mother's bloodstream. These fetal triggers cause the mother to maintain production of progesterone, raise her blood pressure (thereby increasing the volume of blood reaching the fetus), and reduce her control over nutrient flow to the fetus relative to her own tissues (e.g., through placental lactogen, which makes more glucose available to the fetus by counteracting maternal insulin). Pregnancy complications such as pre-eclampsia and gestational diabetes, endangering the life of both mother and fetus, are best known in humans, but there is some evidence for their occurrence in captive great apes and Cercopithecidae (Carter 2007). These problems reflect an extreme outcome of the chemical conflict between fetus and mother. Little is known about the prevalence of such phenomena among wild primates, but among strepsirrhines and plathyrrhines these are expected to be rare, due to their less invasive placentation systems. In general, a

mammal fetus causing severe harm to its mother will have a negligible chance of survival if this harm prevents the mother from providing postnatal nursing care. Thus, the prenatal tug-of-war is likely to favor the mother's survival over that of her helpless offspring.

Developmental Plasticity and Prenatal Effects

On the basis of consistent correlations between low birth weight and the incidence of health problems later in life in humans, Hales and Barker (1992) formulated the thrifty phenotype hypothesis, which initially proposed that inadequate early nutrition has major long-term consequences via impaired development of the endocrine pancreas, which greatly increases susceptibility to type 2 diabetes in adults with abundant access to food. Later research expanded the hypothesis to include adjustments of many physiological settings with lifelong, mainly suboptimal, consequences. These strong effects of early development on later physiological functioning indicate sensitive periods in the development of anatomical and physiological features, as well as limitations on adult responsiveness to environmental changes. These constraints emphasize the role of the environment a mother offers to her offspring.

Physiological priming by conditions experienced during fetal development, now known as metabolic imprinting (Metcalfe & Monoghan 2001), has been demonstrated in many species, from invertebrates to vertebrates (Bateson et al. 2004). Some studies even suggest that a female prenatally affected by her mother's condition in turn affects the condition of her own offspring. For example, captive, single-housed female rhesus monkeys (*Macaca mulatta*) born with low birth weight reached average adult size and weight, but nonetheless produced daughters with low birth weight (Price & Coe 2000). This pattern suggests an intergenerational transmission of fetal growth restrictions, known as gestational imprinting. For humans there are similar indications of this phenotypic inertia (e.g., Gluckman et al. 2005; Kuzuwa 2005).

Prenatal adjustments may be adaptive if the conditions experienced during early development have long-term predictive value (e.g., Bateson 2001, 2008; Gluckman et al. 2007, 2008). For this to occur, such conditions need to persist for a long time relative to an individual's life expectancy. In long-lived species, however, individuals are likely to experience a variety of food conditions over their lifetime, and permanent anatomical or physiological adjustments to unusual food conditions made early in life (such as adjustment of the number of kidney cells or of sensitivity to insulin) thus hold little adaptive potential. Instead, they are likely to reflect a trade-off between the mother's own interests and those of the affected offspring. In general, if early conditions are extreme or relatively temporary, physiological priming probably reflects inevitable trade-offs with long-term consequences (Desai & Hales 1997; Wells 2003, 2007; Bateson et al. 2004). When these effects are carried into the next generation, the trade-off interpretation is even more likely to be correct than the hypothesis that early physiological responses are adaptive.

Studies of humans are beginning to reveal a range of both physiological and behavioral correlates of prenatal and early postnatal exposure to poor nutrition, psychosocial stress, and even physical abuse (e.g., Hales & Barker 2001; Mick et al. 2002; Lahti et al. 2006; Phillips 2007; Entringer et al. 2009; McGowan et al. 2009). Such early exposure appears to have an epigenetic effect—for example, by modifying the expression of steroid receptor genes (Champagne & Curley 2009) or causing stable changes in neuronal networks (Cirulli et al. 2009a). In captive rhesus monkeys, the available milk energy to the infant during the early postnatal period was found to correlate with measurements of the infants' confidence, whereas the level of nutrition during peak lactation had no effect (Hinde & Capitanio 2010), thus suggesting an early fixation of physiological settings. For obvious reasons, little is known about prenatal effects on an individual's physiology as a juvenile or adult in wild primates. However, infant yellow baboons with a low growth rate early in life did not show compensatory growth as weaned immatures when conditions became favorable (Altmann & Albert 2005). In addition, for a cohort of female baboons in the same population, Altmann (1991) found a significant correlation between nutrient acquisition (relative protein and energy intake) as yearlings and reproductive success as adults. This suggests that early conditions and ontogenetic experience, which are both directly affected by the mother and her condition, can have long-term effects on metabolic function. These effects are more consistent with the consequences of maternal tradeoffs than with adaptive responses.

Onyango et al. (2008) reported that fecal glucocorticoid levels of five- to six-year-old male yellow baboons correlated with maternal rank at their conception, which remained unchanged during their first year of life. Since these hormones are involved in the stress response, this pattern suggests that these males suffer chronic stress, which may affect their growth, immunocompetence, and reproduction. This result was unexpected because in this population subadult males, prior to their dispersal from the natal group, rank above all adult females in the dominance hierarchy (Pereira 1988). Maternal glucocorticoid (GC) may directly affect the fetus, the infant through lactation, or the maturing youngster via maternal behavior. Larger data sets are needed to clarify the consistency of the suggested connec-

tion between maternal behavioral environment and sons' stress levels later in life. A cross-fostering approach can help to separate the effects of maternal behavior from other physiological maternal effects. For example, Maestripieri et al. (2007) showed resemblance between infant rejection behavior by foster mothers and that of foster daughters towards their own first offspring, apparently mediated by early adjustment of neuroendocrine settings.

In summary, a primate mother's physiological and behavioral environment may have profound, but largely unexplored, long-term effects on the lives of her offspring. More work is needed to resolve which of these effects are adaptive responses of offspring or outcomes of maternal compromises, such as reduction of investment in pregnancy and lactation under suboptimal circumstances to increase survival for future reproduction (cf. Wells 2003; Baker et al. 2009).

Post-Natal Investment

Lactation and Carrying

Unlike many other mammals, most primate newborns typically cling to their mother and are carried on her body wherever she goes until they are capable of independent locomotion. Thus, most primate mothers not only nourish their offspring with milk, but also carry its increasing weight during their daily travel and foraging (fig. 14.2). In a few haplorrhines (notably callitrichines) and some "monogamous" species (e.g., owl monkeys, *Aotus* spp., and siamang), males or other helpers take over some of the carrying task (see chapter 17, this volume), but nourishment through lactation remains the responsibility of the mother. In contrast, many strepsirrhine mothers leave their young offspring in a nest or tree hole or pick them up orally to transport and then "park" them in ever-changing hiding places while they forage (Kappeler 1998; Ross 2001; chapter 2, this volume).

Fulfilling all the nutritional requirements of an actively moving and growing immature is the most energy-demanding phase of maternal investment, requiring more energy than gestation. Lactation represents more than 75% of the total maternal energy cost of reproduction (Oftedal 1984). Initially the mother provides all nutrition through milk, but this is followed by a sometimes very long transitional period in which milk supplements the infant's own increasing efforts to find, select, and process solid foods. Compared to that of other mammals, the milk of most primates contains a high level of lactose, but little fat and protein (Tilden & Oftedal 1997). This high-lactose milk, which the infant can easily digest, is thought to enable rapid postnatal growth of the primate brain, even though some growth and certainly differentiation of the brain continues throughout the juvenile phase (Martin 1996; Leigh 2004). Thus, primate mothers provide a buffered food supply during the most nutrient-sensitive phase of their offspring's brain development (chapter 10, this volume).

The gross energy density of milk varies only little between different primate species, including the small callitrichines (Power et al. 2002). However, Tilden and Oftedal (1997) found higher proportions of fat and protein in the milk of those strepsirrhines that "park" their offspring while foraging (e.g., lorises, galagos, and some lemurs) than in those that carry their young and allow them to suckle continuously. In parking species, infant growth tends to be relatively fast and mothers' lactation tends to last shorter than gestation (van Schaik & Kappeler 1997; van Schaik et al. 1999; Gursky 2007; Gould & Sauther 2007). On the other hand, female strepsirrhines that carry their infants resemble haplorrhines in several respects, such as milk composition, longer lactation periods, and slower postnatal growth. Thus, primate milk tends to be diluted and provided over a longer period wherever nursing is furnished "on demand" in frequent, short bouts.

Weaning

A mother faces the challenge of finding the moment in her infant's life at which additional investment through milk no longer significantly affects the offspring's success, and can therefore be withheld, even though continued nursing would still benefit it. Figure 14.3 shows how natural selection can set the optimal timing of this termination in investment. This difference between a mother's own optimum and that of her infant suggests it may be in the mother's interest to minimize investment in her current offspring in order to enhance her own survival and future reproductive success, despite putting the survival of the current infant at risk (Trivers 1974; Fairbanks & McGuire 1995). In most primates, high-yield milk production can hardly be combined with simultaneous gestation, and thus the termination of milk provisioning to one offspring coincides, more or less, with the onset of investment in the next. Therefore, the termination of prolonged milk provisioning, known as weaning, is the most conspicuous period of mother-offspring conflict.

Weaning marks the completion of the transition from milk to a solid food diet. To be weaned successfully, an infant needs to be able to digest solid food, travel independently (unless "helpers" relieve the mother of the cost of carrying), and forage competently in the face of moderate fluctuations in food supply. This last requirement ensures

Fig. 14.2. A six-year-old Bornean orangutan (*Pongo pygmaeus*) suckling, illustrating the long exclusive investment made by orangutan females, which exhibit the longest interbirth intervals of all primates. Photo courtesy of Johanna van Schaik.

that the infant has enough food-handling skills to buffer a temporary energy shortage. Thus, the optimal timing of weaning is affected by the infant's mass, age (physiological maturation), and competence in locomotion (in the absence of helpers; see fig. 14.3), food processing, and foraging (recognizing foods). This is especially needed in species whose diets require either complicated foraging skills (i.e., needing practice before efficiency is reached—e.g., hunting, tool use), or knowledge of a vast diversity of food items. Indeed, Jaeggi et al. (2008) showed that infant Bornean orangutans (*Pongo pygmaeus*), who associate almost exclusively with their mothers, have already acquired full knowledge of their mother's diet by the time they are fully weaned at five to seven years of age. Similarly, gorilla (*Gorilla gorilla*) weanlings know the adult diet (Nowell & Fletcher 2008), and weaned immature chimpanzees (*Pan troglodytes*) and Sumatran orangutans (*Pongo abelii*) can use tools common to their populations (Lonsdorf 2005; van Noordwijk & van Schaik 2005). However, chimpanzee males can practice communal hunting skills only from adolescence onwards, since their mothers do not usually participate actively in hunts and thus cannot model this behavior for their sons (Boesch & Boesch-Achermann 2000).

The larger the infant grows, the more its being carried

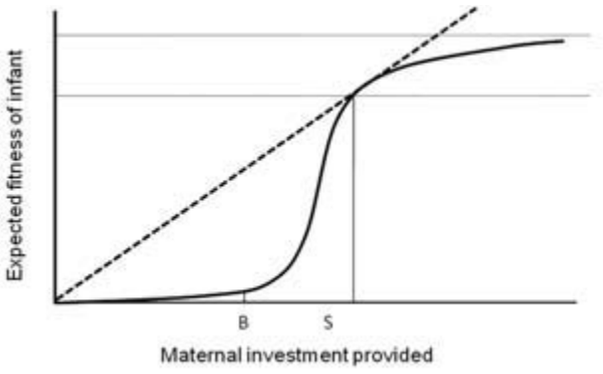

Fig. 14.3. The theoretically optimal moment for the mother to switch (S) her investment from her currently dependent infant to her next offspring, which is equally related to her. For the infant, more investment in itself would contribute more to its expected fitness than the mother's investment into a full- or half-sibling. B indicates the moment of birth.

interferes with the mother's movements, especially during foraging (Altmann 1980). Indeed, several studies have shown that carrying during maternal foraging and resting decreases sooner than during the mother's travel (fig. 14.4), whereas the end of lactation largely coincides with the end of body contact during maternal nonresting activity (e.g., in geladas, *Theropithecus gelada*, Barrett et al. 1995; capuchins, Fragaszy et al. 2004). Carrying the young infant, however, serves not only for transportation but also for thermoregulation. Schino and Troisi (1998) found more attempts to maintain body contact by infant Japanese macaques at lower temperatures. The mothers frequently rejected these attempts, suggesting a rarely noticed mother-offspring conflict over thermoregulation.

There may be a conflict over when the infant is allowed to nurse (Altmann 1980; Barrett et al. 1995), but Bateson (1994) and Barrett et al. (2006) have argued that there is no parent-offspring conflict over the timing of weaning, since the interests of mother and offspring in the infant's survival are the same (see also Maestripieri 2002). In this view, weaning tantrums are honest signals of the offspring's needs, and therefore they reflect an imbalance between those needs and what the mother offers (Barrett & Henzi 2000). This view can be reconciled with classic parent-offspring conflict by considering two different situations. Where immature mortality is largely due to extrinsic factors (predation, disease, infanticide), and thus largely independent of the quality of prolonged maternal investment, infants may be weaned relatively early and sometimes forcefully, which is indicative of conflict (vervets, Hauser 1993; Fairbanks & McGuire 1995; baboons, Lycett et al. 1998). On the other hand, if mortality is strongly affected by care, mothers are expected to invest heavily in each offspring until it can be completely independent (e.g., Drakensberg chacma baboon population: Barrett et al. 2006b). The validity of this argument depends on the extent to which a particular mortality risk is extrinsic and thus affects individuals irrespective of their care-dependent physical condition.

The degree of seasonality of food availability and reproduction may similarly affect the balance between the interests of infant and mother. If gestation and lactation together take about 12 months in a very seasonal environment, an infant requiring just a few months of extra lactation may cause its mother to skip a full reproductive cycle. In primate populations with a less seasonal reproductive schedule or one that easily fits within a seasonal cycle, females will have more flexibility in adjusting their investment to the needs of their current offspring. Here we expect that fluctuations in food availability (either extrinsic or mediated through group size or dominance) affect the duration of lactation and thus interbirth intervals (e.g., long-tailed macaques, van Noordwijk & van Schaik 1999; chacma baboons, Barrett et al. 2006b; Phayre's leaf monkeys, Borries et al. 2008).

Differences in weaning age between populations of baboons (Lycett et al. 1998; Barrett et al. 2006b), gorillas (Nowell & Fletcher 2007), and orangutans (van Noordwijk & van Schaik 2005; van Noordwijk et al. 2009) have been attributed to differences in care-dependent mortality risk. In most cases, however, it remains an open question whether and how a mother can accurately assess her offspring's needs and survival chances, and thus whether her prolonged nutritional investment affects the offspring's chance of success.

Parent-offspring conflict is over the extent of investment and the timing of a mother's switch from investing in the current offspring towards starting her next reproductive effort. Since in primates this transition does not mark the end of mother-offspring association, the severity of the conflict over the timing of this switch is mainly determined by the degree to which an offspring's survival depends on mother's milk as a continued supplement to its nutrition.

Post-Weaning Maternal Care

One of the most striking features of primate development is that weanlings still rely critically for survival on additional low level, nonexclusive support provided during their prolonged postweaning association with the mother and others. Such support can be in the form of (1) protection against inclement weather, predators, and conspecifics, (2) sharing food or other resources or tolerating scrounging, and (3) providing learning opportunities. Females may even

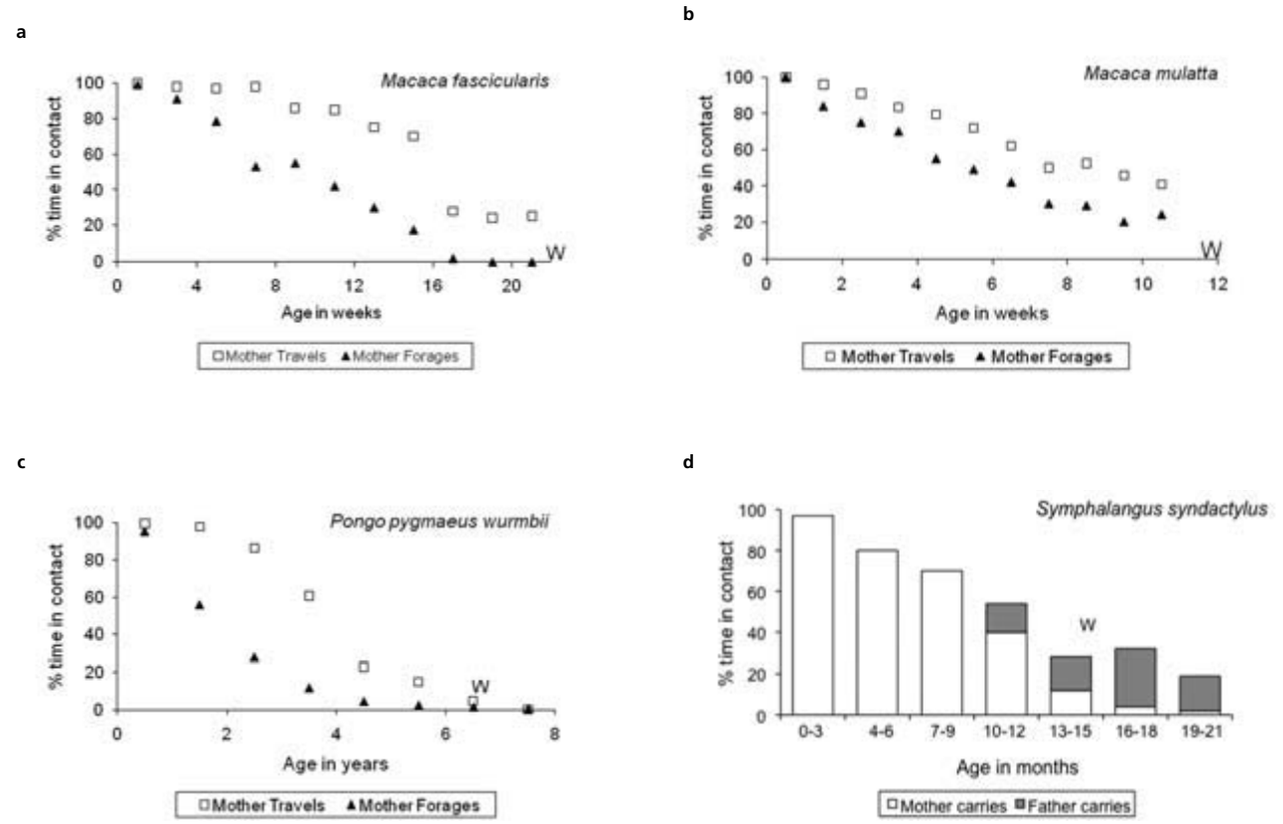

Fig. 14.4. Body contact and/or of an infant at different ages during the mother's travel (true transportation of the infant) and her mostly stationary foraging. Infants tend to reach locomotory independence before weaning (W) in (a) wild, mostly arboreal, long-tailed macaques (*Macaca fascicularis*) in Ketambe (data from Karssemeijer et al. 1990), (b) partly terrestrial rhesus macaques (*M. mulatta*) in a seminatural habitat, Chhatari (data from Johnson 1986), (c) arboreal Bornean orangutans (*Pongo pygmaeus wurmbii*) in Tuanan (data from van Noordwijk et al. unpublished), (d) wild arboreal pair-living siamangs (*Symphalangus syndactylus*) at Way Canguk, in which the father starts to carry the offspring from around the time of weaning (data from Lappan 2008).

provide these forms of care to grand-offspring (Fairbanks 1988, 2000; Pavelka et al. 2009).

In group-living primates, this postweaning association between mother and offspring may last much longer than the preweaning phase, even for youngsters of the dispersing sex. This extended maternal care does not prevent the mother from having subsequent offspring. The resulting simultaneous association of the mother with several immature offspring of different ages—"stacking"—is the rule among diurnal primates, with the notable exception of the orangutan, whose rather solitary lifestyle limits permanent association of a mother to, at most, two immature offspring at a given time (van Noordwijk & van Schaik 2005).

It is difficult to estimate the cost of postweaning care to the mother. Some of the costs potentially are shared with other individuals in the group, in that immatures can follow other group members to food sources and can benefit from their vigilance. The mother may benefit from this arrangement as well, in that she can wean her offspring at a relatively young age before it can survive independently (van Noordwijk & van Schaik 2005).

The value of this continued care to the offspring appears to be appreciable. Although unweaned primate infants generally do not survive the death of their mother (Thierry & Anderson 1986; Fairbanks 2000; Boesch et al. 2010), the fate of weaned immatures orphaned at different ages, relative to their peers, is much less known. Among wild long-tailed macaques, juveniles that lost their mothers after weaning suffered significantly higher mortality (fig. 14.5). In this wild population, with a generally high survival rate (0.66 from birth to four years), the youngest survivors all had a closely related adult female in the group. Thus, mothers apparently provide valuable services beyond those generally obtained from group living. Protection against intragroup competition (via agonistic support) and, perhaps, against thermal challenges during the night (via huddling), are probably more consistently provided by mothers than by other group members.

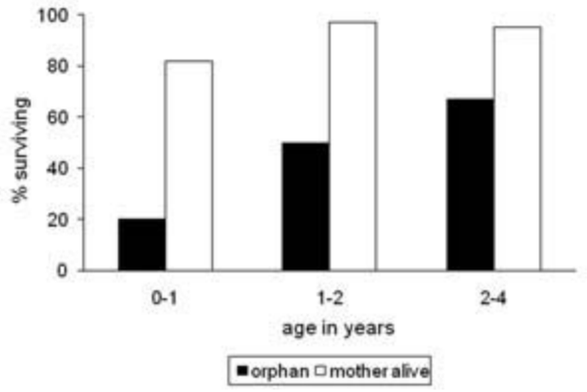

Fig. 14.5. Percentages of orphaned long-tailed macaques that survived to reach the next age cohort after the death of their mothers, compared to immatures with surviving mothers. Survival is lower for orphans whose mothers died after weaning but before they were one year old ($G_{adj}0 = 7.26$, $p < 0.001$), and for those whose mothers died when they were one to two years old ($G_{adj} = 8.36$, $p < 0.01$). But maternal death could affect the survival of three- to four-year-old juveniles as well ($G_{adj} = 2.79$, $p < 0.10$).

Among some primates living in multifemale, unimale groups subject to male takeover events, such as many langurs, weaned immatures may accompany an ousted male (likely their father), when he leaves the natal group and joins an "age-graded-all-male" band, which actually may include immature females (see chapter 19, this volume; fig. 19.7; Hrdy 1977; Rajpurohit & Sommer 1993; Steenbeek et al. 2000). In these species, a physical and social separation between mother and weaned offspring is quite common. Rajpurohit & Sommer (1993) reported that 50% of juvenile Hanuman langurs (*Semnopithecus entellus*) that joined an all-male band died within a year, whether they were living with their putative father or not. Although no formal comparison was presented, this number is likely to be much higher than the mortality rate of mother-associated immatures still living in their natal home range (which may be of higher quality than the range of an all-male band). This comparison supports the notion of the benefits of continued association with the mother.

Certainly, however, survival of juvenile orphans is not uncommon. In such cases (chapter 17, this volume), it could be argued that the prolonged care provided by the mother is not essential. However, even where orphan survival is relatively high, female orphans rarely acquire as high a social status as expected in light of their maternal rank (Hasegawa & Hiraiwa 1980; Johnson 1987; Lee & Johnson 1992; Johnson 2006), although occasionally fraternal support allows them to reach higher rank than expected (chacma baboons: Engh et al. 2009). Lacking competitive support, orphans are also reported to grow at a slower rate (chacma baboons, Johnson 2006). In addition, orphaned female Japanese macaques have lower success in raising their firstborns than do primiparous females with mothers in the group (Hasegawa & Hiraiwa 1980). The presence of the mother is even reported to enhance mating chances of philopatric bonobo sons (*Pan paniscus*, Surbeck et al. 2010), thus suggesting reduced mating success for male orphans. In other species, much less is known about the fate of sons that survive their mother's death, especially after dispersal from the natal group. Alberts and Altmann (1995a) reported that orphan yellow baboon males disperse at a younger age than their peers, but studies of other cercopithecines did not confirm this effect (Kuester & Paul 1999; Fairbanks 2000; van Noordwijk & van Schaik 2001).

The importance of postweaning support from adults is underscored by another phenomenon. Compared with other species, primate immatures arguably have a stronger tendency to maintain an attachment with a primary caregiver well into juvenility. Usually this primary caregiver is the mother, but in her absence it can be another (usually related) female, an older sibling, or an adult or subadult male with whom the orphan spends as much time in proximity and grooming as it would have done with its mother (Japanese macaques, Hasegawa & Hiraiwa 1980; Nozaki 2009; white-faced capuchins, Perry 2008; chimpanzees, Boesch et al. 2010). Orphans play an active role in maintaining such mother-replacing relationships: they adopt their caregivers more persistently than vice versa, and just as with the mother-offspring relationship, such adopted bonds may last a lifetime, at least among females (Yamada et al. 2005; Nakamichi & Yamada 2007). Even male caretakers frequently accept adoptions (but not always: Boesch et al. 2010). For example, a gorilla orphan tends to be adopted by its putative father, who will share a nest with it (Stewart 2001; Yamagiwa & Kahekwa 2001), and male chimpanzees may do the same (Boesch et al. 2010). If immature adoptees are almost weaned at the time of the mother's death, they seem to have a good chance of survival at least until maturity (chimpanzees, Watts & Pusey 1993, Boesch et al. 2010; ursine howler monkeys, *Aloutta arctoidea*, Pope 2000; chacma baboons, Engh et al. 2001; Japanese macaques, Nozaki 2009). Although the benefits to the young immatures of such relationships seem obvious, no studies have yet shown a significant effect on orphan survival. Even less is known about the benefits, and particularly the costs, to caregivers.

Overall, current data suggest that in primates, offspring with a prolonged mother-offspring association have better chances of survival and reproduction, and thus selection is expected for the mother's survival, which could benefit not only her youngest offspring, but her older ones and other maternal kin as well.

Allomaternal Support: Who Cares, and How?

In dispersed, relatively solitary primates such as orangutans and some nocturnal strepsirrhines, mothers are the sole source of support for their offspring. In many gregarious species, particularly those living in bisexual, multifemale societies, membership in a social group provides mothers and offspring with some shareable benefits, such as enhanced predator detection and access to food. Several recent studies have shown a strong correlation between a female's reproductive parameters (especially offspring survival) and the number of her adult maternal relatives in the group (e.g., ursine howler monkeys, Pope 2000; chacma baboons, Cheney et al. 2006; white-faced capuchin monkeys, Fedigan et al. 2008) or the number of close associates (baboons, Silk et al. 2003; 2009; Japanese macaques, Pavelka et al. 2009). Even though the support provided by these relatives differs between species, these data suggest that primate mothers benefit from a social network to raise their offspring. This effect can be seen as an extension of the maternal effects discussed in the previous section.

Primate mothers and immatures can also receive direct, targeted attention from certain group members in the form of babysitting, carrying, allonursing, and provisioning. When mothers mutually provide allonursing and perhaps other forms of care to each other's offspring, we speak of *communal breeding*. In principle, communal care can be exchanged and more or less fairly reciprocated among mothers. When mothers and offspring receive extensive care from nonmothers—that is, males and nonreproductive adults or subadults—we speak of *cooperative* breeding. To test whether seemingly helpful behavior actually constitutes care, either the mother or the offspring should have enhanced reproduction or survival when more help is received.

In species with a strict dominance hierarchy, mothers are often reluctant to let others, especially non-kin, handle their offspring (Chism 2000). Nevertheless, other adult females and immatures of either sex in particular are attracted to young infants and try to get access to them through grooming the mother (e.g. Muroyama 1994; Henzi & Barret 2002), whereupon they handle the infants and even carry them away from their mothers. This does not occur specifically when such transportation is needed, however, and low-ranking mothers have difficulty retrieving infants from dominant handlers (Chism 2000). Fairbanks (1990) suggested that vervet monkey infant handlers themselves benefit by gaining experience. However, in her study of bonnet macaques (*Macaca radiata*), Silk (1999) found no clear benefits to infant handlers, mothers, or infants, and therefore concluded that infant handling is most likely a by-product of selection for natal attractivity to enlist appropriate maternal care. Thus, infant carrying by others than the mother in hierarchically structured primate groups probably cannot be considered care, since it does not relieve the mother from providing care (cf. Hrdy 1976).

In some species, temporary aggregations of same-aged infants can be found near just one or a few vigilant females while the other mothers concentrate on foraging without being distracted or hindered by their active infant (e.g., Nilgiri black langur, *Semnopithecus johnii*, Poirier 1968; patas monkeys, vervet, guenons, Chism 2000). However, despite some indications that this crèche-allocare may enable females to achieve a shorter interbirth interval (Fairbanks 1990), it is still unclear whether all mothers take turns and benefit equally from such shared child supervision. In some colobines, juvenile helpers (who tend to be at least paternally related) carry infants during long-distance travel (Kirkpatrick 2007; Xi et al. 2008), but it is not yet clear how valuable this allocarrying is for the mother or her offspring. Thus, in many species the real value of infant carrying for the mother (reduced investment), the infant (increased chances of survival), or the caregiver (improved maternal skills), as well as the degree of reciprocity involved (communal care), are largely unresolved.

Allonursing is a form of allocare with a clear energetic cost (milk) to the provider. This has been reported for strepsirrhines (gray mouse lemurs, *Microcebus murinus*, Eberle & Kappeler 2006; silky sifakas, *Propithecus candidus*, Patel 2007), New World monkeys (ursine howler monkeys, Pope 2000; capuchins, Fragaszy et al. 2004; squirrel monkeys, Soltis et al. 2005), and several Old World monkeys (guenons, patas, talapoin monkeys, Chism 2000; colobines, Kirkpatrick 2007), but rarely among macaques, baboons, and great apes. Since only other lactating mothers can provide allonursing, the potential for reciprocity is clear. Occasionally some allonursing is provided by females who have not given birth (e.g., ring-tailed lemurs, Pereira & Izard 1989) or who have lost their own infants (Bolivian squirrel monkeys, *Saimiri boliviensis*, Milligan et al. 2008).

If mothers are equally likely to provide some allonursing to each other's infants, they don't gain or lose net energy from this form of communal care, but might gain foraging efficiency in not having to stay in permanent close proximity to their infants (Eberle & Kappeler 2006; Perry 2008). However, in populations of different capuchin species, low-ranking mothers nursed infants of high-ranking mothers more often than vice versa, thus suggesting an uneven advantage (O'Brien 1988; Perry 1996; Baldovino & di Bitetti 2006).

True allocare that reduces the amount of energy a mother expends on carrying her relatively heavy offspring is found

in species living in single-female groups (e.g., siamangs, Lappan 2008; spectral tarsier, Gursky 2000). A comparison of siamang groups with different levels of male care showed that mothers that received more carrying help from their male partners had shorter interbirth intervals (Lappan 2008, 2009). In a small number of primates that tend to give birth to twins or even triplets, male partners of the mother do most of the carrying and provisioning (Callitrichines: Bales et al. 2002; Fite et al. 2005). Mothers may carry and retrieve their offspring even less when the available helpers are experienced at allocare (Fite et al. 2005).

Females in such cooperative breeding systems compete heavily over access to helpers. This competition may be shown by overt aggression or harassment of other females, thereby limiting group membership, suppressing other females' reproductive physiology, or even killing subordinate females' newborns (see chapter 15, this volume, fig. 15.5; Digby 2000; common marmoset, *Callithrix jacchus*, Saltzman et al. 2009). However, breeding females are also reported to disproportionally groom the females that help them, which can be interpreted as an incentive to keep them in the group as caregivers (common marmoset, Lazaro-Perea et al. 2004). Thus, successful reproduction of females in cooperative breeding primates has become completely dependent on allocare, and recruiting helpers is an essential component of reproduction for these females (fig. 14.6). As

Fig. 14.6. Allomaternal care is especially pronounced in the callitrichines. For example, callitrichine twin infants are carried most of the time during their first three to four weeks of life, but other group members, such as this adult male moustached tamarin (*Saguinus mystax*) in Peru, relieve mothers of much of the cost of this activity. Photo courtesy of Julia Diegmann.

a consequence, mothers have an extended conflict of interest with their own weaned offspring, who are unable to reproduce in their natal group. Older offspring can either provide allocare for siblings, which is in the mother's interest, or try to find a breeding position in another group, which may be even more costly to them than helping their mother (e.g., saddle-back tamarin, *Saguinus fuscicollis*, Goldizen et al. 1996). Only one daughter can take over the mother's support group upon her death, typically after a reproductive tenure of only a few years. Thus, whereas the outcome of mother-infant conflict over investment depends on the mother's access to sufficient help, her conflict with her sexually mature offspring depends on demographic conditions.

Comparative analyses (Mitani & Watts 1997; Ross & MacLarnon 2000; Ross 2003) have suggested that species with some form of allocare (such as guarding, carrying, or allonursing) have faster infant growth and shorter interbirth intervals than species that lack such help. However, because infants of species with allocare are not larger as weanlings and do not start reproduction earlier than those without allocare, it was concluded that almost all allocare can be interpreted as being beneficial for the mother, but not directly beneficial for individual infants. Yet a direct survival benefit to allocare for infants is suggested by within-species comparisons of the level of received allocare in obligate cooperative breeders. These species show a high risk of maternal abandonment of infants when helpers are lacking (several Callitrichine species, Santos et al. 1997; Bardi et al. 2001). In addition, orphaned gray mouse lemur and white-faced capuchin monkey infants, living in settings with a relatively high level of allonursing, appear to have increased chances of survival through adoption by their allomothers, although sample sizes remain small (Eberle & Kappeler 2006; Perry 2008). Such enhancement of offspring survival would benefit both the mother and the offspring—although, as with all insurance policies, only a few individuals reap the benefits.

In conclusion, in at least some primate species a mother's minimally required investment in an offspring, as well as her reproductive success, depend on the quality and quantity of the allocare her offspring receives, which in turn largely depends on her own social relationships. An infant's chance of survival may improve in the presence of allocaregivers (in cooperative breeders) or allomothers (in communal breeders). More importantly, perhaps, in both communal and cooperative breeders a mother can decrease the amount of care she gives her offspring in response to the level of allocare received, and thus she can save energy for investment in her next offspring—whereas the infant's physical development is hardly affected by allocare. In species with despotic female hierarchies, true allocare is relatively rare due to the potential for very uneven distribution of the benefits.

Maternal Investment in Sons and Daughters

If unequal numbers of females and males are present in a population, mothers producing offspring of the rarer sex benefit by obtaining more grand-offspring, which will drive the secondary sex ratio toward equality (Fisher 1930). Thus, equal investment in sons and daughters is expected. However, many studies on wild mammals have found deviations from an equal sex ratio (Clutton-Brock & Iason 1986; Sheldon & West 2004). The reason is that individual females may achieve greater reproductive success via offspring of one sex because their social position or age differentially affects either the costs of raising sons or daughters or the expected reproductive success of these offspring.

Several hypotheses identify benefits to mothers of biasing their investment according to the sex of their offspring. The Trivers-Willard (1973) hypothesis predicts that females will bias the sex ratio according to differences in their ability to enhance the future reproductive success of sons versus daughters. The local resource competition (LRC) hypothesis posits that mothers will bias the sex ratio of their offspring in favor of the dispersing sex (usually male in primates). This is because adults of the philopatric sex (usually female) compete over food and other resources with their own mothers (as well as their sisters), thereby reducing both their mothers' ability to reproduce and their own (Clark 1978). However, if offspring of the philopatric sex improve their mother's additional reproduction (e.g., directly through allocare in cooperatively breeding species or indirectly through matriline size effects), then the mothers are expected to bias sex ratios toward the philopatric sex as per the local resource enhancement (LRE) hypothesis (Emlen et al. 1986).

Silk and Brown (2008) found that the adult size dimorphism of a species, which is often used as a proxy for the relative energy costs of raising sons versus daughters, was not independently correlated with the average birth sex ratio in that species. In primate species in which the conditions of LRC apply, females give birth to significantly more offspring of the dispersing sex (Johnson 1988; Silk & Brown 2008), whereas in LRE species with cooperative breeding, the birth sex ratio is biased towards the helping sex. Even though these results suggest adaptive deviations from the expected 1:1 sex ratio for the average conditions for species, they may mask further fine-tuning at the population or individual level. For example, van Schaik & Hrdy (1991) pointed out that the severity of local competition may vary both within and between populations (as well as with provisioning or captive conditions), and that this may explain why the costs and benefits of differential investment could vary even within populations. In a meta-analysis, Schino

(2004) indeed found a clear effect of food availability on birth sex ratios in different primate populations. Nunn and Pereira (2000) also found evidence for fine-tuning within a species. Their study of one provisioned population of ring-tailed lemurs suggested both LRE and LRC effects on offspring sex ratio. Females that had just formed a new group (through fission) and young females that received targeted aggression preceding expulsion overproduced daughters that could serve as potential allies (LRE). At the population level, however, females tended to overproduce dispersing sons at larger group sizes (LRC). Thus, multiple factors affect the potential benefits to mothers of differential investment in sons and daughters, and under different conditions, different pressures may prevail (cf. Cockburn et al. 2002).

The facultative sex ratio adjustment hypothesis of Trivers and Willard (1973) assumes not only that the variance in reproductive success is higher for one sex (usually males, in polygynous animals) but also that the mother's condition (including her physical, nutritional, and social status) during the investment period differentially influences the future reproductive success of her sons and daughters. Thus, mothers in good condition are expected to overproduce high-quality sons with high reproductive success prospects, whereas mothers in poor condition would have more grand-offspring if they overproduce daughters whose reproductive success is less affected by their quality.

For primates, we still lack quantitative evidence that maternal condition (or, more likely, dominance rank as a proxy for ability to garner food or protect offspring) during the offspring's early development differentially affects the later reproductive success of sons and daughters. Obviously, this assumption is difficult to test in long-lived species in which there is a long delay between weaning and the onset of reproduction, and in which accurate lifetime reproductive data are typically much harder to collect for members of the dispersing sex than for the philopatric sex. In primates with female philopatry, the expected reproductive future of daughters is similar to that of their mothers under ecologically and socially stable conditions. A mother's influence on her son's reproductive prospects, however, is usually limited because she can effectively support her immature sons only up to a certain size, above which agonistic support from a female no longer meaningfully affects male-male competition outcomes (bonobos may be an exception: Surbeck et al. 2010). In some cercopithecines, the sons of high-ranking mothers mature faster and enjoy better physical condition in early adulthood than do the sons of low-ranking females (Alberts & Altmann 1995a, b; Bercovitch et al. 2000; Setchell et al. 2001; Garcia et al. 2009). Such developmental advantages may well enhance these males' reproductive success after successful dispersal, as has been reported for long-tailed macaques (van Noordwijk & van Schaik 1999, 2001). However, the same high-ranking females also produce daughters with reproductive advantages (see also Johnson 2003; Altmann & Alberts 2005); thus, the differential payoff of biased investment in sons is still unclear.

Biased sex ratios at birth reflect biased early investment, possibly mediated by sex-biased early abortion under the influence of glucose and hormone levels (Grant 2007; James 2007; Cameron et al. 2008). Some epigenetic consequence of adverse conditions during early development may also affect sons and daughters differently (Price & Coe 2000; Cirulli et al. 2009b). Also, females could bias their postnatal investment in sons and daughters, resulting in different interbirth intervals. For example, the duration and energy costs of maternal care of unweaned offspring are greater for sons than for daughters in chimpanzees (Nishida et al. 2003), mountain gorillas (Robbins et al. 2007), Hanuman langurs, (Ostner et al. 2005), rhesus macaques (Bercovitch et al. 2000), and gray mouse lemurs (Colas 1999). This sex difference in early investment may, however, be counterbalanced by compensatory maternal care later in life in philopatric female offspring, where daughters (and their offspring) receive disproportionately more grooming and agonistic support than do sons (Fairbanks 1988).

In summary, at the species level systematic deviations from an equal sex ratio at birth consistent with the predictions of the LRC and LRE hypotheses have been shown. Fine-tuning of this adjustment at the population or individual level may contribute to seemingly inconsistent results. In most cases, however, it remains an open question how much primate mothers influence their sons' lifetime reproductive success, whereas a mother's long-lasting impact on her daughters' reproduction is well documented, at least in groups with matrilineal hierarchies. This makes it still hard to test Trivers and Willard's hypothesis of maternal condition effects on offspring sex ratio in primates.

From Maternal Investment to Lifetime Maternal Care?

Primate mothers bestow on their offspring lifelong physiological maternal effects, reflecting the outcome of a mother-offspring conflict over investment affected by the mother's condition during the offspring's early development. However, all primate mothers also maintain individualized relationships with their weaned offspring and other members of their social group, or with neighbors in adjacent ranges. On the other hand, there is much variation among primates in the extent of care provided to immatures by mothers and others, whether offspring of both sexes disperse, or whether mothers maintain lifelong associations with adult daughters

(in many primates) or sons (in, for example, chimpanzees and bonobos: Stumpf 2007).

Prolonged maternal association may be beneficial to the young offspring, but it is not parental investment in that it does not directly reduce a mother's future reproduction. At least where group living is ecologically beneficial, the mother's costs of extended association with offspring are low—and if the extended association does benefit the offspring, the mothers also derive inclusive fitness benefits. The same would be true for association and care extended to other relatives. Females in species with despotic matrilineal hierarchies that regulate access to food and safety benefit most from strong supportive bonds, and their offspring benefit from receiving prolonged protection against other group members. Here a mother's dominance rank can affect her daughters' early reproductive success, and daughters acquire their own dominance rank with matrilineal support (fig. 14.7). Thus, daughters benefit from a strong bond with their mothers, but the mothers may benefit from associating with their daughters as well, through agonistic support or other supportive social interactions. The benefits for a female's reproductive success of extended association and matrilineal bonds may be so high that, in the absence of maternal kin, a female invests in establishing and maintaining a limited number of strong replacement bonds (Silk et al. 2006a, b), which may even help her to overcome the disadvantages of low dominance rank (Silk et al. 2009). Thus, prolonged mother-offspring care may have given rise to similar relationships among other dyads, using the same bonding mechanism (grooming exchange and agonistic support) to obtain similar reproductive benefits.

Fig. 14.7. One of the most significant features of maternal care in primates is the prolonged association with adult offspring, especially daughters, and the resultant opportunities for continued support. Here, a mother-and-daughter pair of white-faced capuchin monkeys (*Cebus capucinus*) at Santa Rosa, Costa Rica, have formed a coalition against a rival female. Photo courtesy of Susan Perry.

Long life span and individualized social relationships may have facilitated the development of strong, lifelong bonds between mothers and their offspring, with mutual benefits. Similar long-lasting bonds are found in some nonprimate gregarious mammals (e.g., elephants, *Loxodonta africana*, Archie et al. 2006). In most mammals, however, females provide one-sided maternal investment in offspring, which is accompanied by conflict over the level and continuation of investment. Primate mothers tend to live in social settings in which the period of minimally required maternal investment is followed by an extended association, which for the philopatric sex lasts a lifetime. These associations enable lifelong, mutually supportive bonds that benefit both mothers and their offspring. Thus, in at least some primates, the quality of a female's lifelong maternal care may well be an important component of her reproductive success.

Summary and Conclusions

In this chapter I have examined some of the patterns and variables affecting maternal investment and care among primates. For example, variation is found in the timing of reproduction relative to more or less predictable changes in food abundance. With lengthening of the reproductive cycle (conception to weaning) and decreasing predictability in food supply, mothers are more likely to store fat reserves to ensure sufficient nutrient supply to their dependent offspring. Thus, primate species vary in their patterns of maternal physiology, and in the likelihood and timing of reproductive failure. In addition, the value of a mother's continued investment for the survival of the offspring affects the flexibility in the timing of her termination of maternal investment. Furthermore, maternal effects triggered during early development can have lifelong physiological consequences. In the long-lived primates, these seem to reflect a compromise between the mother's physical and social condition and the offspring's demands, and they indicate sensitive developmental periods followed by limits to physiological plasticity later in life.

Finally, with their relatively slow development and tendency to have a gregarious lifestyle, primate mothers not only invest in their offspring through gestation and lactation, but also maintain a long-lasting association with their weaned offspring, during which maternal care is still valuable to the offspring. This bond may still award benefits during young adulthood for offspring of the nondispersing sex.

References

Alberts, S. & Altmann, J. 1995a. Balancing costs and opportunities: Dispersal in male baboons. *American Naturalist*, 145, 279–306.

———. 1995b. Preparation and activation: determinants of age at reproductive maturity in male baboons. *Behavioral Ecology and Sociobiology*, 36, 397–406.

Altmann, J. 1980. *Baboon Mothers and Infants*. Cambridge, MA: Harvard University Press.

Altmann, J. & Alberts, S. C. 2003. Variability in reproductive success viewed from a life-history perspective in baboons. *American Journal of Human Biology*, 15, 401–409.

———. 2005. Growth rates in a wild primate population: ecological influences and maternal effects. *Behavioral Ecology and Sociobiology*, 57, 490–501.

Altmann, S. A. 1991. Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. *Proceedings of the National Academy of Sciences USA*, 88, 420–423.

Archie, E. A., Moss, C. J. & Alberts, S. C. 2006. The ties that bind: Genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B*, 273, 513–522.

Bainbridge, D. R. J. 2000. Evolution of mammalian pregnancy in the presence of the maternal immune system. *Reviews of Reproduction*, 5, 67–74.

Baker, J., Hurtado, A. M., Pearson, O. M., Hill, K. R., Jones, T. & Frey, M. A. 2009. Developmental plasticity in fat patterning of Ache children in response to variation in interbirth intervals: A preliminary test of the roles of external environment and maternal reproductive strategies. *American Journal of Human Biology*, 21, 77–83.

Baldovino, M. C. & Di Bitetti, M. S. 2008. Allonursing in tufted capuchin monkeys (*Cebus nigritus*): Milk or pacifier? *Folia Primatologica*, 79, 79–92.

Bales, K., French, J. A. & Dietz, J. M. 2002. Explaining variation in maternal care in a cooperatively breeding mammal. *Animal Behaviour*, 63, 453–461.

Bardi, M., Petto, A. J. & Lee-Parritz, D. E. 2001. Parental failure in captive cotton-top tamarins (*Saguinus oedipus*). *American Journal of Primatology*, 54, 159–169.

Barrett, L., Dunbar, R. I. M. & Dunbar, P. 1995. Mother-infant contact as contingent behaviour in gelada baboons. *Animal Behaviour*, 49, 805–810.

Barrett, L., Halliday, J. & Henzi, S. P. 2006a. The ecology of motherhood: The structuring of lactation costs by chacma baboons. *Journal of Animal Ecology*, 75, 875–886.

Barrett, L. & Henzi, S. P. 2000. Are baboon infants Sir Phillip Sydney's offspring? *Ethology*, 106, 645–658.

Barrett, L., Henzi, S. P. & Lycett, J. E. 2006b. Whose life is it anyway? Maternal investment, developmental trajectories, and life history strategies in baboons. In *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives* (ed. by L. Sweddell & S. R. Leigh) 199–224. New York: Springer.

Bateson, P. 1994. The dynamics of parent-offspring relationships in mammals. *Trends in Ecology & Evolution*, 9, 399–403.

———. 2001. Fetal experience and good adult design. *International Journal of Epidemiology*, 30, 928–934.

———. 2008. Preparing offspring for future conditions is adaptive. *Trends in Endocrinology and Metabolism,* 19, 111.

Bateson, P., Barker, D., Clutton-Brock, T., Deb, D., D'Udine, B., Foley, R. A., Gluckman, P., Godfrey, K., Kirkwood, T., Mirazon Lahr, M., McNamara, J., Metcalfe, N. B., Monaghan, P., Spencer, H. G. & Sultan, S. E. 2004. Developmental plasticity and human health. *Nature*, 430, 419–421.

Bearder, S. K. 1999. Physical and social diversity among nocturnal primates: A new view based on long term research. *Primates*, 40, 267–282.

Bercovitch, F. B. 1987. Female weight and reproductive condition in a population of olive baboons (*Papio anubis*). *American Journal of Primatology*, 12, 189–195.

Bercovitch, F. B. & Berard, J. D. 1993. Life history costs and consequences of rapid reproductive maturation in female rhesus macaques. *Behavioral Ecology and Sociobiology*, 32, 103–109.

Bercovitch, F. B. & Strum, S. C. 1993. Dominance rank, resource availability, and reproductive maturation in female savanna baboons. *Behavioral Ecology and Sociobiology*, 33, 313–318.

Bercovitch, F. B., Widdig, A. & Nürnberg, P. 2000. Maternal investment in rhesus macaques (*Macaca mulatta*): Reproductive costs and consequences of raising sons. *Behavioral Ecology and Sociobiology*, 48, 1–11.

Boesch, C. & Boesch-Achermann, H. 2000. *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution*. Oxford: Oxford University Press.

Boesch, C., Bole, C., Eckhardt, N. & Boesch, H. 2010. Altruism in forest chimpanzees: The case of adoption. *PlosOne*, 5, e8901.

Borries, C., Larney, E., Lu, A., Ossi, K. & Koenig, A. 2008. Costs of group size: Lower developmental and reproductive rates in larger groups of leaf monkeys. *Behavioral Ecology*, 19, 1186–1191.

Boyd, I. L. 2000. State-dependent fertility in pinnipeds: Contrasting capital and income breeders. *Functional Ecology*, 14, 623–630.

Brockman, D. K. & van Schaik, C. P. 2005. Seasonality and reproductive function. In *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates* (ed. by D. K. Brockman & C. P. van Schaik), 269–305. Cambridge: Cambridge University Press.

Broussard, D. R., Dobson, F. S. & Murie, J. O. 2005. The effects of capital on an income breeder: Evidence from female Columbian ground squirrels. *Canadian Journal of Zoology*, 83, 546–552.

Cameron, E. Z., Lemons, P. R., Bateman, P. W. & Bennett, N. C. 2008. Experimental alteration of litter sex ratios in a mammal. *Proceedings of the Royal Society B*, 275, 323–327.

Carter, A. M. 2007. Animal models of human placentation: A review. *Placenta*, 28, Supplement A, Trophoblast Research, 21, S41–S47.

Champagne, F. A. & Curley, J. P. 2009. Epigenetic mechanisms mediating the long-term effects of maternal care on development. *Neuroscience and Biobehavioral Reviews*, 33, 593–600.

Cheney, D. L. & Seyfarth, R. M. 1987. The influence of intergroup competition on the survival and reproduction of female vervet monkeys. *Behavioral Ecology and Sociobiology*, 21, 375–386.

Cheney, D. L., Seyfarth, R. M., Andelman, S. J. & Lee, P. C. 1988. Reproductive success in vervet monkeys. In *Reproductive Success* (ed. by T. H. Clutton-Brock), 384–402. Chicago: University of Chicago Press.

Cheney, D. L., Seyfarth, R. M., Fischer, J., Beehner, J., Bergman, T., Johnson, S. E., Kitchen, D. M., Palombit, R. A., Rendall, D. & Silk, J. B. 2004. Factors affecting reproduction and mortality among baboons in the Okavango delta, Botswana. *International Journal of Primatology*, 25, 401–428.

Cheney, D. L., Seyfarth, R. M., Fischer, J., Beehner, J. C., Bergman, T. J., Johnson, S. E., Kitchen, D. M., Palombit, R. A., Rendall, D. & Silk, J. B. 2006. Reproduction, mortality, and female reproductive success in chacma baboons of the Okavango Delta, Botswana. In *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives* (ed. by L. Swedell & S. R. Leigh), 147–176. New York: Springer.

Chism, J. 2000. Allocare patterns among cercopithecines. *Folia Primatologica*, 71, 55–66.

Cirulli, F., Francia, N., Berry, A., Aloe, L., Alleva, E. & Suomi, S. J. 2009a. Early life stress as a risk factor for mental health: Role of neurotrophins from rodents to non-human primates. *Neuroscience and Biobehavioral Reviews*, 33, 573–585.

Cirulli, F., Francia, N., Branchi, I., Antonucci, M. T., Aloe, L., Suomi, S. J. & Alleva, E. 2009b. Changes in plasma levels of BDNF and NGF reveal a gender-selective vulnerability to early adversity in rhesus macaques. *Psychoneuroendocrinology*, 34, 172–180.

Clark, A. B. 1978. Sex ratio and local resource competition in a prosimian primate. *Science*, 201, 163–165.

Clutton-Brock, T.H. 1991. *The Evolution of Parental Care*. Princeton, NJ: Princeton University Press.

Clutton-Brock, T. H. & Iason, G. R. 1986. Sex ratio variation in mammals. *Quarterly Review of Biology*, 61, 339–374.

Cockburn, A., Legge, S. & Double, M. C. 2002. Sex ratios in birds and mammals: Can the hypotheses be disentangled? In *Sex Ratios: Concepts and Research Methods* (d. by Hardy, I. C. W.), 266–286. Cambridge: Cambridge University Press.

Colas, S. 1999. Evidence for sex-biased behavioral maternal investment in the gray mouse lemur (*Microcebus murinus*). *International Journal of Primatology*, 20, 911–926.

Desai, M. & Hales, N. 1997. Role of fetal and infant growth in programming metabolism in later life. *Biological Reviews*, 72, 329–248.

Digby, L. 2000. Infanticide by female mammals: Implications for the evolution of social systems. In *Infanticide by Males and its implications* (ed. by C. P. van Schaik & C. H. Janson), 423–446. Cambridge: Cambridge University Press.

Drent, R. H. & Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea*, 68, 225–252.

Dunbar, R. I. M. 1988. *Primate Social Systems*. Ithaca, NY: Cornell University Press.

Eberle, M. & Kappeler, P. M. 2006. Family insurance: Kin selection and cooperative breeding in a solitary primate (*Microcebus murinus*). *Behavioral Ecology and Sociobiology*, 60, 582–588.

Emlen, S. T., Emlen, J. M. & Levin, S. A. 1986. Sex-ratio selection in species with helpers-at-the-nest. *American Naturalist*, 127, 1–8.

Engh, A. L., Hoffmeier, R. R., Seyfarth, R. M. & Cheney, D. L. 2009. O brother, where art thou? The varying influence of older siblings in rank acquisition by female baboons. *Behavioral Ecology and Sociobiology*, 64, 97–104.

Entringer, S., Kumsta, R., Hellhammer, D. H., Wadhwa, P. D. & Wüst, S. 2009. Prenatal exposure to maternal psychosocial stress and HPA axis regulation in young adults. *Hormones & Behavior*, 55, 292–298.

Fairbanks, L. A. 1988. Vervet monkey grandmothers: Interactions with infant grandoffspring. *International Journal of Primatology*, 9, 425–441.

———. 1990. Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour*, 40, 553–562.

———. 2000. Maternal investment throughout the life span in Old World monkeys. In *Old World Monkeys* (ed. by P. F. Whitehead & C. J. Jolly), 341–367. Cambridge: Cambridge University Press.

Fairbanks, L. A. & McGuire, M. T. 1995. Maternal condition and the quality of maternal care in vervet monkeys. *Behaviour*, 132.

Fedigan, L. M., Carnegie, S. D. & Jack, K. M. 2008. Predictors of reproductive success in female white-faced capuchins (*Cebus capucinus*). *American Journal of Physical Anthropology*, 137, 82–90.

Festa-Bianchet, M., Gaillard, J.-M. & Jorgenson, J. T. 1998. Mass-and density-dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist*, 152, 367–379.

Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Oxford University Press.

Fite, J. E., Patera, K. J., French, J. A., Rukstalis, M., Hopkins, E. C. & Ross, C. N. 2005. Opportunistic mothers: Female marmosets (*Callithrix kuhlii*) reduce their investment in offspring when they have to, and when they can. *Journal of Human Evolution*, 49, 122–142.

Fragaszy, D. M., Fedigan, L. M. & Visalberghi, E. 2004. *The Complete Capuchin: The Biology of the Genus Cebus*. Cambridge: Cambridge University Press.

Garcia, C., Lee, P. C. & Rosetta, L. 2009. Growth in colony living anubis baboon infants and its relationship with maternal activity budgets and reproductive status. *American Journal of Physical Anthropology*, 138, 123–135.

Gluckman, P. D., Hanson, M. A. & Beedle, A. S. 2007. Early life events and their consequences for later disease: A life history and evolutionary perspective. *American Journal of Human Biology*, 19, 1–19.

Gluckman, P. D., Hanson, M. A., Beedle, A. S. & Spencer, H. G. 2008. Predictive adaptive responses in perspective. *Trends in Endocrinology and Metabolism*, 19, 108–110.

Gluckman, P. D., Hanson, M. A., Spencer, H. G. & Bateson, P. 2005. Environmental influences during development and their later consequences for health and disease: Implications for the interpretation of empirical studies. *Proceedings of the Royal Society B*, 272, 671–677.

Goldizen, A. W., Mendelsohn, J., van Vlaardingen, M. & Terborgh, J. 1996. Saddle- back tamarin (*Saguinus fuscicollis*) reproductive strategies: Evidence from a thirteen-year study of a marked population. *American Journal of Primatology*, 38, 57–83.

Gould, L. & Sauther, M. 2007. Lemuriformes. In *Primates in Perspective* (ed. by C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger & S. K. Bearder), 46–72. Oxford: Oxford University Press.

Gould, L., Sussman, R. W. & Sauther, M. L. 2003. Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. *American Journal of Physical Anthropology*, 120, 182–194.

Grant, V. J. 2007. Could maternal testosterone levels govern mammalian sex ratio deviations? *Journal of Theoretical Biology*, 246, 708–719.

Gursky, S. 2007. Tarsiiformes. In *Primates in Perspective* (ed. by C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger & S. K. Bearder), 73–85. Oxford: Oxford University Press.

———. 2000. Allocare in a nocturnal primate: Data on the spectral tarsier, *Tarsius spectrum*. *Folia Primatologica*, 71, 39–54.

———. 2002. The behavioral ecology of the spectral tarsier, *Tarsius spectrum*. *Evolutionary Anthropology*, 11, 226–234.

Haig, D. 1993. Genetic conflicts in human pregnancy. *Quarterly Review of Biology*, 68, 495–532.

Hales, C. N. & Barker, D. J. P. 1992. Type 2 (non-insulin-dependent) diabetes mellitus: The thrifty phenotype hypothesis. *Diabetologia*, 35, 595–601.

———. 2001. The thrifty phenotype hypothesis. *British Medical Bulletin*, 60, 5–20.

Hasegawa, T. & Hiraiwa, M. 1980. Social interactions of orphans observed in a free-ranging troop of Japanese monkeys. *Folia Primatologica*, 33, 129–158.

Hauser, M. D. 1993. Do vervet monkey infants cry wolf? *Animal Behaviour*, 45, 1242–1244.

Henzi, S. P. & Barrett, L. 2002. Infants as a commodity in a baboon market. *Animal Behaviour*, 63, 915–921.

Hinde, K. & Capitano, J. P. 2010. Lactational Programming? Mother's milk energy predicts infant behavior and temperament in rhesus macaques (*Macaca mulatta*). *American Journal of Primatology*, 71, 1–8.

Hrdy, S.B. 1976. Care and exploitation of nonhuman primate infants by conspecifics other than the mother. *Advances in the Study of Behavior*, 6, 101–158

———. 1977. *The Langurs of Abu: Female and Male Strategies of Reproduction*. Cambridge, MA: Harvard University Press.

Iverson, S. J., Oftedal, O. T., Bowen, W. D., Boness, D. J. & Sampugna, J. 1995. Prenatal and postnatal transfer of fatty acids from mother to pup in the hooded seal. *Journal of Comparative Physiology B*, 165, 1–12.

Jaeggi, A. V., van Noordwijk, M. A. & van Schaik, C. P. 2008. Begging for information: Mother-offspring food sharing among wild Bornean orangutans. *American Journal of Primatology*, 70, 533–541.

James, W. H. 2008. Some comments on the paper of Grant (2007). *Journal of Theoretical Biology*, 253, 401–404.

Janson, C. & Verdolin, J. 2005. Seasonality of primate births in relation to climate. In *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates* (ed. by D. K. Brockman & C. P. van Schaik), 307–350. Cambridge: Cambridge University Press.

Johnson, C. N. 1988. Dispersal and the sex ratio at birth in primates. *Nature*, 332, 726–728.

Johnson, J. A. 1987. Dominance rank in juvenile olive baboons, *Papio anubis*: The influence of gender, size, maternal rank and orphaning. *Animal Behaviour*, 35, 1694–1708.

Johnson, R. L. 1986. Mother-infant contact and maternal maintenance activities among free-ranging rhesus monkeys. *Primates*, 27, 191–203.

Johnson, S. E. 2003. Life history and the competitive environment: Trajectories of growth, maturation, and reproductive output among chacma baboons. *American Journal of Physical Anthropology*, 120, 83–98.

———. 2006. Maternal characteristics and offspring growth in chacma baboons: A life history perspective. In *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives* (ed. by L. Swedell, L. & S.R. Leigh), 177–197. Oxford: Oxford University Press.

Kappeler, P. M. 1998. Nests, tree holes, and the evolution of primate life histories. *American Journal of Primatology*, 46, 7–33.

Karssemeijer, G. J., Vos, D. R. & van Hooff, J. A. R. A. M. 1990. The effect of some non-social factors on mother-infant contact in long-tailed macaques (*Macaca fascicularis*). *Behaviour*, 113, 273–291.

Kavanagh, M. & Laursen, E. 1984. Breeding seasonality among long-tailed macaques, *Macaca fascicularis*, in peninsular Malaysia. *International Journal of Primatology*, 5, 17–29.

Kawai, M. 1965. On the system of social ranks in a natural troop of Japanese monkeys, 1: Basic rank and dependent rank. In *Japanese Monkeys* (ed. by K. Imanishi, K. & S.A. Altmann), 66–86. Atlanta: Emory University Press.

Kirkpatrick, R. C. 2007. The Asian colobines. Diversity among leaf-eating monkeys. In *Primates in Perspective* (ed. by C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger & S. K. Bearder), 186–200. Oxford: Oxford University Press.

Kurita, H., Sugiyama, Y., Ohsawa, H., Hamada, Y. & Watanabe, K. 2008. Changes in demographic parameters of *Macaca fuscata* at Takasakiyama in relation to decrease of provisioned foods. *International Journal of Primatology*, 29, 1189–1202.

Kuzuwa, C. W. 2005. Fetal origins of developmental plasticity: Are fetal cues reliable predictors of future nutritional environments? *American Journal of Human Biology*, 17, 5–21.

Laengin, K. M., Norris, D. R., Kyser, T. K., Marra, P. P. & Ratcliffe, L. M. 2006. Capital versus income breeding in a migratory passerine bird: Evidence from stable-carbon isotopes. *Canadian Journal of Zoology*, 84, 947–953.

Lahti, J., Räikkönen, K., Kajantie, E., Heinonen, K., Pesonen, A.-K., Järvenpää, A. L. & Strandberg, T. 2006. Small body size at birth and behavioural symptoms of ADHD in children aged five to six years. *Journal of Child Psychology and Psychiatry*, 47, 1167–1174.

Lappan, S. 2008. Male care of infants in a siamang (*Symphalangus syndactylus*) population including socially monogamous and polyandrous groups. *Behavioral Ecology and Sociobiology*, 62, 1307–1317.

Lappan, S. 2009. The effects of lactation and infant care on adult energy budgets in wild siamangs (*Symphalangus syndactylus*). *American Journal of Physical Anthropology*, 140, 290–301.

Lazaro-Perea, C., De Fatima Arruda, M. & Snowdon, C. T. 2004. Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Animal Behaviour*, 67, 627–636.

Lee, P. C. & Johnson, J. A. 1992. Sex differences in alliances, and the acquisition and maintenance of dominance status among immature primates. In *Coalitions and Alliances in Humans and Other Animals* (ed. by A. H. Harcourt & F. B. M. de Waal), 391–414. Oxford: Oxford University Press.

Leigh, S. R. 2004. Brain growth, life history, and cognition in

primate and human evolution. *American Journal of Primatology*, 62, 139–164.
Lewis, R. J. & Kappeler, P. M. 2005. Are Kirindy sifaka capital or income breeders? It depends. *American Journal of Primatology*, 67, 365–369.
Lonsdorf, E. V. 2005. Sex differences in the development of termite-fishing skills in wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*, 70, 673–683.
Lycett, J. E., Henzi, S. P. & Barrett, L. 1998. Maternal investment in mountain baboons and the hypothesis of reduced care. *Behavioral Ecology and Sociobiology*, 42, 49–56.
Martin, R. D. 1990. *Primate Origins and Evolution: A Phylogenetic Reconstruction*. London: Chapman & Hall.
———. 1996. Scaling of the mammalian brain: The maternal energy hypothesis. *News in Physiological Science*, 11, 149–156.
———. 2008. Evolution of placentation in primates: Implications of mammalian phylogeny. *Evolutionary Biology*, 35, 125–145.
Mas-Rivera, A. & Bercovitch, F. B. 2008. Postpartum recuperation in primiparous rhesus macaques and development of their infants. *American Journal of Primatology*, 70, 1047–1054.
McGowan, P. O., Sasaki, A., D'Alessio, A. C., Dymov, S., Labonté, B., Szyf, M., Turecki, G. & Meaney, M. J. 2009. Epigenetic regulation of the glucocorticoid receptor in human brain associates with childhood abuse. *Nature Neuroscience*, 12, 342–348.
Metcalfe, N. B. & Monaghan, P. 2001. Compensation for a bad start: Grow now, pay later? *Trends in Ecology and Evolution*, 16, 254–260.
Mick, E., Biederman, J., Prince, J., Fischer, M. J. & Farafone, S. V. 2002. Impact of low birth weight on attention-deficit hyperactivity disorder. *Journal of Developmental & Behavioral Pediatrics*, 23, 16–22.
Milligan, L. A., Gibson, S. V., Williams, L. E. & Power, M. L. 2008. The composition of milk from Bolivian squirrel monkeys (*Saimiri boliviensis boliviensis*). *American Journal of Primatology*, 70, 35–43.
Mitani, J. C. & Watts, D. 1997. The evolution of non-maternal caretaking among anthropoid primates: Do helpers help? *Behavioral Ecology and Sociobiology*, 40, 213–220.
Moore, T. & Haig, D. 1991. Genomic imprinting in mammalian development: A parental tug-of-war. *Trends in Genetics*, 7, 45–49.
Muroyama, Y. 1994. Exchange of grooming for allomothering in female patas monkeys. *Behaviour*, 128, 103–119.
Nakamichi, M. & Yamada, K. 2007. Long-term grooming partnerships between unrelated adult females in a free-ranging group of Japanese monkeys (*Macaca fuscata*). *American Journal of Primatology*, 69, 652–663.
Nievergelt, C. M. & Martin, R. D. 1999. Energy intake during reproduction in captive common marmosets (*Callithrix jacchus*). *Physiology and Behaviour*, 65, 849–854.
Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., Hunt, K. D., Itoh, N., Kawanaka, K., Matsumoto-Oda, A., Mitani, J. C., Nakamura, M., Norikoshi, K., Sakamaki, T., Turner, L., Uehara, S. & Zamma, K. 2003. Demography, female life history, and reproductive profiles among chimpanzees of Mahale. *American Journal of Primatology*, 59, 99–121.
Nowell, A. A. & Fletcher, A. W. 2008. The development of feeding behaviour in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behaviour*, 145, 171–193.
Nozaki, M. 2009. Grandmothers care for orphans in a provisioned troop of Japanese macaques (*Macaca fuscata*). *Primates*, 50, 85–88.
Nunn, C. L. & Pereira, M. E. 2000. Group histories and offspring sex ratios in ringtailed lemurs (*Lemur catta*). *Behavioral Ecology and Sociobiology*, 48, 18–28.
O'Brien, T. G. 1988. Parasitic nursing behavior in the wedge-capped capuchin monkey (*Cebus olivaceus*). *American Journal of Primatology*, 16, 341–344.
Oftedal, O. T. 1984. Milk composition, milk yield, and energy output at peak lactation: A comparative review. *Symposia of the Zoological Society of London, 51*, 33–85.
Onyango, P. O., Gesquiere, L. R., Wango, E. O., Alberts, S. C. & Altmann, J. 2008. Persistence of maternal effects in baboons: Mother's dominance rank at son's conception predicts stress hormone levels in subadult males. *Hormones & Behaviour*, 54, 319–324.
Ostner, J., Borries, C., Schuelke, O. & Koenig, A. 2005. Sex allocation in a colobine monkey. *Ethology*, 111, 924–939.
Ottoni, E. B., de Resende, B. D. & Izar, P. 2005. Watching the best nutcrackers: What capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Animal Cognition*, 8, 215–219.
Parker, G. A., Royle, N. J. & Hartley, I. R. 2002. Intrafamilial conflict and parental investment: A synthesis. *Philosophical Transactions Royal Society London B*, 357, 295–307.
Patel, E. R. 2007. Non-maternal infant care in wild Silky sifakas (*Propithecus candidus*). *Lemur News*, 12, 39–42.
Pavelka, M. S. M., Fedigan, L. M. & Zohar, S. 2009. Availability and adaptive value of reproductive and postreproductive Japanese macaque mothers and grandmothers. *Animal Behaviour*, 64, 407–414.
Pereira, M. E. 1988. Agonistic interactions of juvenile savannah baboons. I. Fundamental features. *Ethology 79*, 195–217.
———. 1993. Seasonal adjustments of growth rate and adult body weight in ringtailed lemurs. In *Lemur Social Systems and their Ecological Basis* (ed. by P. M. Kappeler & J. U. Ganzhorn). 205–221. New York: Plenum.
Perry, S. 1996. Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology*, 40, 167–182.
———. 2008. *Manipulative Monkeys: The Capuchins of Lomas Barbudal*. Cambridge, MA: Harvard University Press.
Phillips, D. I. W. 2007. Programming of the stress response: A fundamental mechanism underlying the long-term effects of the fetal environment? *Journal of Internal Medicine*, 261, 453–460.
Poirier, F. E. 1968. The Nilgiri langur *(Presbytis johnii)* mother-infant dyad. Primates, 9, 45–68
Pope, T. R. 2000. Reproductive success increase with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behavioral Ecology and Sociobiology*, 48, 253–267.
Power, M. L., Oftedal, O. T. & Tardif, S. D. 2002. Does the milk of Callitrichid monkeys differ from that of larger Anthropoids? *American Journal of Primatology*, 56, 117–127.

Price, K. C. & Coe, C. L. 2000. Maternal constraint on fetal growth patterns in the rhesus monkey (*Macaca mulatta*): The intergenerational link between mothers and daughters. *Human Reproduction*, 15, 452–457.

Rahpurohit, L. S. & Sommer, V. 1993. Juvenile male emigration from natal one-male troops of hanuman langurs. In *Juvenile Primates: Life History, Development, and Behavior* (ed. by M. E. Pereira & L.A. Fairbanks), 86–103. Oxford: Oxford University Press.

Rapaport, L. G. & Brown, G. R. 2008. Social influences on foraging behavior in young nonhuman primates: Learning what, where, and how to eat. *Evolutionary Anthropology*, 17, 189–201.

Rasmussen, D. T. 1985. A comparative study of breeding seasonality and litter size in eleven taxa of captive lemurs (*Lemur* and *Varecia*). *International Journal of Primatology*, 6, 501–517.

Richard, A. F., Dewar, R. E., Schwartz, M. & Ratsirarson, J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology London*, 256, 421–436.

Robbins, A. M., Robbins, M. M. & Fawcett, K. 2007. Maternal investment of the Virunga Mountain Gorillas. *Ethology*, 113, 235–245.

Ross, C. 2001. Park or ride? Evolution of infant carrying in primates. *International Journal of Primatology*, 22, 749–771.

———. 2003. Life history, infant care strategies, and brain size in primates. In *Primate Life Histories and Socioecology* (ed. by P. M. Kappeler & M. E. Pereira), 266–284. Chicago: University of Chicago Press.

Ross, C. & MacLarnon, A. 2000. The evolution of non-maternal care in anthropoid primates: A test of the hypotheses. *Folia Primatologica*, 71, 93–113.

Saltzman, W., Digby, L. J. & Abbott, D. H. 2009. Reproductive skew in female common marmosets: What can proximate mechanisms tell us about ultimate causes? *Proceedings of the Royal Society B*, 276, 389–399.

Santos, C. V., French, J. A. & Otta, E. 1997. Infant carrying behavior in callitrichid primates: *Callithrix* and *Leontopithecus*. *International Journal of Primatology*, 18, 889–907.

Schiml, P. A., Mendoza, S. P., Saltzman, W., Lyons, D. M. & Mason, W. A. 1999. Annual physiological changes in individually housed squirrel monkeys (*Saimiri sciureus*). *American Journal of Primatology*, 47, 93–103.

Schino, G. 2004. Birth sex ratio and social rank: Consistency and variability within and between primate groups. *Behavioral Ecology and Sociobiology*, 15, 850–856.

Schino, G. & Troisi, A. 1998. Mother-infant conflict over behavioral thermoregulation in Japanese macaques. *Behavioral Ecology and Sociobiology*, 43, 81–86.

Setchell, J. M., Lee, P. C., Wickings, E. J. & Dixson, A. F. 2001. Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). *American Journal of Physical Anthropology*, 115, 349–360.

———. 2002. Reproductive parameters and maternal investment in mandrills (*Mandrillus sphinx*). *International Journal of Primatology*, 23, 51–68.

Sheldon, B. C. & West, S. A. 2004. Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. *American Naturalist*, 163, 40–54.

Silk, J. B. & Brown, G. R. 2008. Local resource competition and local resource enhancement. *Proceedings of the Royal Society B*, 275, 1761–1765.

Silk, J. B., Alberts, S. C. & Altmann, J. 2003. Social bonds of female baboons enhance infant survival. *Science*, 302, 1231–1234.

Silk, J. B., Willoughby, E. & Brown, G. R. 2005. Maternal rank and local resource competition do not predict birth sex ratios in wild baboons. *Proceedings of the Royal Society B*, 272, 859–864.

Silk, J. B., Altmann, J. & Alberts, S. C. 2006a. Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, 61, 183–195.

Silk, J. B., Alberts, S. C. & Altmann, J. 2006b. Social relationships among adult female baboons (*Papio cynocephalus*). II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, 61, 197–204.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2009. The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B*, 276, 3099–3104.

Soltis, J., Wegner, F. H. & Newman, J. D. 2005. Urinary prolactin is correlated with mothering and allo-mothering in squirrel monkeys. *Physiology & Behaviour*, 84, 295–301.

Stearns, S. C. 1992. *The Evolution of Life Histories.* Oxford: Oxford University Press.

Steenbeek, R., Sterck, E. H. M., de Vries, H. & van Hooff, J. A. R. A. M. 2000. Costs and benefits of the one-male, age-graded and all-male phase in wild Thomas's langur groups. In *Primate Males* (ed. by P. M. Kappeler), 130–145. Cambridge: Cambridge University Press.

Stewart, K. 2001. Social relationships of immature gorillas and silverbacks. In *Mountain Gorillas: Three Decades of Research of Karisoke* (ed. by M. M. Robbins, P. Sicotte & K. J. Stewart), 183–213. Cambridge: Cambridge University Press.

Stumpf, R. 2007. Chimpanzees and bonobos: Diversity within and between species. In *Primates in Perspective* (ed. by C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger & S. K. Bearder), 321–344. New York: Oxford University Press.

Sugiyama, Y. & Ohsawa, H. 1982. Population dynamics of Japanese monkeys with special reference to the effect of artificial feeding. *Folia Primatologica*, 39, 238–263.

Surbeck, M., Mundry, R. Hohmann, G. 2010. Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proceedings of the Royal Society B*, 278, 590–598.

Tardif, S. D. & Jacuish, C. E. 1997. Number of ovulations in the marmoset monkey (*Callithrix jacchus*): Relation to body weight, age and repeatability. *American Journal of Primatology*, 42, 323–329.

Thierry, B. & Anderson, J. R. 1986. Adoption in anthropoid primates. *International Journal of Primatology*, 7, 191–216.

Tilden, C. D. & Oftedal, O. T. 1997. Milk composition reflects pattern of maternal care in prosimian primates. *American Journal of Primatology*, 41, 195–211.

Trivers, R. L. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man.* (ed. by B. Campbell), 136–179. Chicago: Aldine.

———. 1974. Parent-offspring conflict. *American Naturalist*, 14, 249–264.

Trivers, R. L. & Willard, D. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179, 90–92.

Van Noordwijk, M. A. & van Schaik, C. P. 1999. The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. *Primates*, 40, 105–130.

———. 2001. Career moves: Transfer and rank challenge decisions by male long-tailed macaques. *Behaviour*, 138, 359–395.

———. 2005. Development of ecological competence in Sumatran orangutans. *American Journal of Physical Anthropology*, 127, 79–94.

Van Noordwijk M. A., Sauren S. E. B., Nuzuar, Abulani A., Morrogh-Bernard H. C., Utami Atmoko S. S. & van Schaik C. P. 2009. Development of independence: Sumatran and Bornean orangutans compared. In *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (ed. by S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia & C. P. van Schaik), 189–203. New York: Oxford University Press.

Van Schaik, C. P. 1983. Why are diurnal primates living in groups? *Behaviour*, 87, 120–144.

———. 1989. The ecology of social relationships amongst female primates. In *Comparative Socioecology* (ed. by V. Standen & R. A. Foley), 195–218. Oxford: Blackwell.

Van Schaik, C. P. & Hrdy, S. B. 1991. Intensity of local resource competition shapes the relationship between maternal rank and sex ratios at birth in cercopithecine primates. *American Naturalist*, 138, 1555–1562.

Van Schaik, C. P. & Kappeler, P. M. 1997. Infanticide risk and the evolution of male-female association in primates. *Proceedings of the Royal Society B*, 264, 1687–1694.

Van Schaik, C. P. & Paul, A. 1996. Male care in primates: Does it ever reflect paternity? *Evolutionary Anthropology*, 5, 152–156.

Van Schaik, C. P., Terborgh, J. W. & Wright, S. J. 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, 24, 353–377.

Van Schaik, C. P. & van Noordwijk, M. A. 1985. Interannual variability in fruit abundance and reproductive seasonality in Sumatran long-tailed macaques (*Macaca fascicularis*). *Journal of Zoology*, 206, 533–549.

Van Schaik, C. P., van Noordwijk, M. A. & Nunn, C. L. 1999. Sex and social evolution in primates. In *Comparative Primate Socioecology* (ed. by P. C. Lee), 204–240. Cambridge: Cambridge University Press.

Warner, D. A., Bonnet, X., Hobson, K. A. & Shine, R. 2008. Lizards combine stored energy and recently acquired nutrients flexibly to fuel reproduction. *Journal of Animal Ecology*, 77, 1242–1249.

Watanabe, K., Mori, A. & Kawai, M. 1992. Characteristic features of the reproduction of Koshima monkeys, *Macaca fuscata fuscata*: A summary of thirty-four years of observation. *Primates*, 33, 1–32.

Watts, D. P. & Pusey, A. E. 1993. Behavior of juvenile and adolescent great apes. In *Juvenile Primates. Life History, Development, and Behavior* (ed. by M. E. Pereira & L. A. Fairbanks), 148–167. Oxford: Oxford University Press.

Wells, J. C. K. 2003. The thrifty phenotype hypothesis: Thrifty offspring or thrifty mother? *Journal of Theoretical Biology*, 221, 143–161.

———. 2007. Flaws in the theory of predictive adaptive responses. *Trends in Endocrinology and Metabolism*, 18, 331–337.

Wheatley, K. E., Bradshaw, C. J. A., Harcourt, R. G. & Hindell, M. A. 2008. Feast or famine: Evidence for mixed capital-income breeding strategies in Weddell seals. *Oecologia*, 155, 11–20.

Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, 75, 262–299.

Xi, W. Z., Li, B. G., Zhao, D. P., Hi, W. H. & Zhang, P. 2008. Benefits to female helpers in wild *Rhinopithecus roxellana*. *International Journal of Primatology*, 29, 593–600.

Yamada, K., Nakamichi, M., Shizawa, Y., Yasuda, J., Imakawa, S., Hinobayashi, T. & Minami, T. 2005. Grooming relationships of adolescent orphans in a free-ranging group of Japanese macaques (*Macaca fuscata*) at Katsuyama: A comparison among orphans with sisters, orphans without sisters, and females with a surviving mother. *Primates*, 46, 145–150.

Yamagiwa, J. & Kahekwa, J. 2001. Dispersal patterns, group structure, and reproductive parameters of eastern lowland gorillas at Kahuzi in the absence of infanticide. In *Mountain Gorillas. Three Decades of Research at Karisoke* (ed. by M. M. Robbins, P. Sicotte & K. J. Stewart), 91–122. Cambridge: Cambridge University Press.